4. THE LIFE CYCLE OF APHIDS AND COCCIDS.*

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APHIDS.

To attempt to epitomize the life cycle of the aphid is like trying to draw an orderly sketch of Chaos. But after all, the confusion may be more seeming than real and certain rules, beset though they may be with exceptions, govern the life of even the aphid.

The gamogenetic egg is an outstanding argument for the conclusion that the aphid of the North is holding more closely to its prehistoric past than are those that spend their lives where the successive seasons of the year offer a constant source of food. For in the region of real winters there is no member of the family Aphididæ (in its restricted sense) whose total life history has been worked out, that is known to pass its annual cycle without exhibiting a concluding generation comprising both sexes. The aphid, then, starts its life cycle like a typical insect—in the fertilized egg.

The overwintering egg is thus true to the traditions of the Hexapods, but with it ends all conventional observances, for between one such egg and the next in sequence there are crowded such phenomena as a succession of parthenogenetic viviparous generations; extreme examples of polymorphism; alternation of generations in a series where a duplication may not occur for seven or more generations; parallel series in which certain females give birth to true sexes without beaks while others of the same generation give rise to normal young which hibernate in the first instar without feeding; and a system of seasonal migration which is not surpassed by any other in the animal kingdom. That all these divergences from the ordinary life cycle for insects take place within the limits of the family Aphididæ would seem remarkable indeed; but it is no less than appalling to realize that the total range of phenomena just indicated may be exhibited by a single species.

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*These groups share with other Hemiptera the general heterometabolic or "gradual" metamorphosis, but present a bewildering array of specializations and adaptations.

Papers from the Maine Agricultural Experiment Station: Entomology No.106.

For the purpose of illustrating such a cycle, which will give a representation of the family in the complex estate which many of its members have attained, we might focus our attention on that common, widespread, and well known aphid, *Eriosoma lanigera*, with reference to the outline, Chart II.

I. APHIDIDÆ.

FORMS AND SEQUENCE OF GENERATIONS TYPICAL FOR MIGRATING APHIDS.*

I. Fundatrix	(4)	apterous, parthenogenetic, viviparous female—hatching from the overwintering egg and living on primary host.
II. Spuriæ apteræ	(1)	parthenogenetic, viviparous females—living on primary host.
III. Spuriæ alatæ	(1)	parthenogenetic, viviparous females—developing on primary host and migrating to secondary host.
IV. Spuriæ apteræ	(2)	parthenogenetic, viviparous females—developing on secondary host.
V. Sexuparæ alatæ	(3)	parthenogenetic, viviparous females—developing on secondary host migrating to primary host.
VI. Sexuales		males (4) and oviparous (4) females.
I. Eggs	(4)	on primary host.

(1) The second and third generations, with certain species, may comprise both apterous and alate females; or there may be several generations of either the apterous or the alate females.

(2) There may be two or more generations like IV which are usually counterparts of II.

(3) The fall migrants may resemble III closely or they may differ markedly.

(4) These appear but once in the annual cycle.

* The terms applied to the different aphid forms are very numerous. A tabulation of these for uniform reference would be interesting and convenient but too detailed to be in keeping with this brief paper.

The beautifully elaborated relation of this insect to the nature of its environment, and more the way in which it controls and selects its environment, results in a life history the events of which are as thrilling as a tale of enchantment. The stem-mother touches the unfolding elm leaf with her wizard beak and the magic castle appears with its ample shelter. Its living wells throb with the sap of growth from which the witch drinks and becomes the giant mother of two or three hundred sireless daughters born at the season when sap runs freely and growth is easy. These in turn give birth to unfathered daughters threatened with disaster. A thousand hungry beaks drain the castle wells of their sap. The floors run with honey dew, and

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II. LIFE CYCLE OF *Eriosoma lanigera*. WOOLLY APHID OF THE APPLE.

Seven Generations.

May..........I. Stem-mother (hatching from overwintering egg; causing and developing in rosetted leaf cluster of American Elm).

June..........II. Apterous viviparous female (developing in elm-leaf rosette).

June–July......III. Alate viviparous female (spring migrant flying from elm to apple).

July..........IV. Apterous viviparous female (developing on stem of water-shoot or tender bark of apple).

August........V. Apterous viviparous female (developing on bark of apple—branch or root).

September.....

VI. Apterous viviparous female remaining on apple bark.	VI. Alate viviparous female. Fall migrant flying from apple to elm.
VII. Overwintering nymph, hibernating about crown of apple tree.	VII. Apterous beakless male and Apterous beakless oviparous female.
	I. Overwintering egg in crevice of elm bark.

(This outline is in accordance with the Maine schedule, in which connection it might be stated that the overwintering nymphs are, for the most part, a luckless lot. *Prociphilus tessellata*, however, which exhibits similar parallel cycles brings through the hibernating nymphs with much success).

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mold appears. The murderous gangs of capsid, beetle and syrphid enter. And lo, the aphid but unfurls her migrant wings and seeks the juicy stem of an apple, clean and unknown to the enemies of her kind. Her daughters, lacking the leafy shelter of the elm, throw between them and the sun a waxy fluff and thrive. But her great-granddaughters find the bark of the apple less generous for their needs, and their ancient enemies have smelled their blood and come to slaughter under the roof of wax. And then the migrant, true to the instincts of the clan in the hour of need, quietly escapes and bears the torch of life home to the elm. This voyage of the fall migrant seems inexplicable. It is neither her hunger nor that of her unborn brood that urges her forth for neither she nor her dwarfed, beakless progeny feed on the elm. It is not a quest for a mate, for she, like her maternal ancestors for five generations, gives parthenogenetic birth to her young. But, whatever the cause, once and once only in seven generations the fall migration takes

III. Hormaphidini. Life Cycle of *Hormaphis hamamelidis*.
(Three generations).

I.	Fundatrix	apterous viviparous female; hatching from overwintering egg; causing and developing within the witch hazel gall; reproducing by parthenogenesis.
II.	Sexuparæ alatæ	Alate viviparous females; developing within the witch hazel gall; dispersing to witch hazel leaves; reproducing by parthenogenesis.
III.	Sexuales	dwarf, apterous male and oviparous female; both with beaks developing on witch hazel leaves; female laying several fertilized eggs.
I.	Eggs	overwintering on witch hazel.

(For the vicinity of New York, adapted in part from T. H. Morgan and A. F. Shull)

place from secondary to primary host, as once and once only in seven generations the reverse migration of the spring occurs.

Any one such life cycle as that just indicated, though representative, must be specific rather than comprehensive.

An inter-food-plant migration would seem to have become typical of the Aphididæ, for it is met in ten* or more widely distributed tribes; although in many instances the migration is restricted to fresh plants of the same species, a modification that obscures its significance.

That the environment is influential in the production of the winged forms, thus giving the mechanism for migration, is

*Aphidini, Myzini, Macrosiphini, Anoeciini, Mindarini, Schizoneurini, Prociphilini, Pemphigini, Hormaphidini, Pterocommini.

IV. CHERMISINA.* (Life Cycle Typical for Chermes).

	Primary Host, Picea	Intermediate Host, Larix (or Pinus or Abies)
1st Year	I. Fundatrices (hibernate—cause galls—wingless, all ♀ II. Alatæ Non migrantes (larvæ inhabit gall—adults winged, all ♀ Migrantes	
2nd Year	I. Fundatrices (as before) V. Sexuales (wingless—cause no gall) II. Alate (as before) Non-migrantes Migrantes to Larix (as before)	III. Colonici (hibernate—cause no gall—wingless, all ♀ larvæ live on the needles—cause no gall all ♀ IV. Sexuparæ (adults winged) Exsules (adults wingless) Exsules
	I. Fundatrices I. Fundatrices	?

* No longer included with the family Aphididæ in its restricted sense.

(Adapted from E. R. Burdon, Proceedings of the Cambridge Philosophical Society, Vol. XIII, Pt. 1).

indicated by the circumstance that the best defined examples of migration are exhibited by gregarious species and is correlated with the exhaustion by the aphids of the infested food-plant in the spring and with either that or a normal ripening of the food-plant in the fall. The evidence of Shinji, based upon food tests under chemical control appear to be of especial significance in this respect.

V. PHYLLOXERINÆ.* Life Cycle Typical for the Phylloxerans.

I. Stem-mother (apterous female; hatching from the overwintering egg; causing the gall on hickory and developing within it; laying eggs that develop parthenogenetically).

II. alate female (developing in gall; laying a number of eggs on hickory that develop parthenogenetically to males).	II. alate female (developing in gall laying a number of eggs on hickory that develop parthenogenetically to sexual females).
III. male (apterous, dwarfed, beakless).	III. sexual female (apterous, dwarfed, beakless; laying a single fertilized egg).

I. winter egg (on branch of hickory).

* No longer included with the Family Aphididæ in its restricted sense.

Although the testimony of aphids in the North emphasizes the annual occurrence of the fertilized egg, the parthenogenetic reproduction, which is characteristic for all but a single annual generation, may in many species be indefinitely continued in a warm climate or in hot house conditions (as witness Ewing's 87 generations with *Aphis avenæ*). Whether temperature is the direct control in such cases may be doubted for we have many species producing both alate and apterous forms throughout the summer; and it may be that the continual vegetable growth made possible by the warm climate is the direct encouragement to parthenogenetic viviparous reproduction. This supposition is accentuated by the fact that even in tropical climates experiencing a wet and a dry season gamogenetic eggs are produced to tide over the period of famine; and in the North some non-migrating species produce the sexes in August, July or even June on exhausted vegetation.

The parthenogenetic type of reproduction, correlated, as it were, with the abbreviated time required for the development of the individual, makes possible the enormous increase of the aphid colony and at the same time minimizes the numerical importance of the gamogenetic egg. We find, then, one of the very striking differences between these and other insects, in the fact that the oviparous female of the aphid never deposits more than a few eggs and in certain tribes one egg only of this character is produced. As if to further emphasize the significance of parthenogenesis for the aphid, certain species (as *Eriosoma lanigera* and *Prociphilus tessellata*) even when dwelling in the North, attempt to provide for a continuation of the apterous, viviparous, parthenogenetic part of their cycle by producing annually nymphs to hibernate about the base of the secondary host at the same time that the migrants are producing the sex forms on the primary host.*

COCCIDS.

The eccentricities of the coccids are concerned with the specialization of their structural characters, and the modified metamorphosis of both sexes rather than with any striking range of habit or peculiarity in sequence of generations; since their typical life cycle comprises between one fertilized egg stage and the next but a single generation composed of both sexes. The extreme possibilities of coccid metamorphosis are illustrated by those species in which the females, at their first molt, lose, for good and all, eyes, antennæ and legs, exhibiting in this atrophy of those organs of orientation and locomotion, a trans-

*In the preparation of this paper repeated attempts have been made to broach the aphid cycle in general terms, a process that would force us to build upon a hypothetical type reminiscent of a primitive condition when each generation was composed of males and females, both alate, and when propagation was solely by means of the gamogenetic egg as is typical for the class Insecta; but not only is such a lost type hypothetical for the aphids, but the processes of divergence have been so marvelously complicated, as concerns structure, habit, and sequence and combination of generations, that the hope of correlating the different groups on any graphic basis has been abandoned; and representative glimpses are all that the accompanying outlines offer.

Appreciative thanks are due Dr. A. C. Baker, Dr. O. W. Oestlund and Dr. Herbert Osborn for reading the paper critically and for certain suggestions that have been incorporated.

formation which has to do with the loss of such organs as characterized them as insects in the first instar, rather than in the acquisition and development of the structures of an adult hexapod. This metamorphosis by reduction, associated with the complete absence of wing development in the female is correlated with the sedentary habit of this family and is in line

VI. COCCIDÆ. Generalized Outline.*

Male	*Female*
1st Instar active	1st Instar active
2nd Instar Xylococcinæ active. Monophlœbinæ active. Eriococcinæ active to near end of period. Diaspinæ quiescent.	2nd Instar active or fixed.
3rd Instar Xylococcinæ quiescent. Monophlœbinæ active. Eriococcinæ quiescent. Diaspinæ quiescent.	3rd Instar active or fixed. Diaspinæ adult.
4th Instar Xylococcinæ quiescent. Monophlœbinæ quiescent. Eriococcinæ quiescent. Diaspinæ quiescent.	4th Instar Xylococcus fixed. Monophlœbinæ adult. Eriococcinæ adult.
5th Instar Xylococcinæ quiescent. Monophlebinæ adult. Eriococcinæ adult. Diaspinæ adult.	5th Instar Xylococcus adult.
6th Instar Xylococcinæ adult.	

* This outline is given by courtesy of Dr. A. D. MacGillivray, to whom thanks are also due for a critical reading of the Coccid part of the present paper and for certain suggestions that have been incorporated.

with the atrophy of class structures in parasitic animals. But the suppression of generalized characters does not inhibit the appearance of special structures of a high degree of development, as is beautifully illustrated by the wax glands, marvelous in form and variety, to be found in the coccids; a concentration of structural effort directed toward the secretion of a waxy protection for these sedentary creatures and their eggs.

VII. COCCIDÆ. Life Cycle of *Xylococcus betulæ.*

Fertilized Eggs.

Male and Female

1st Instar—Indistinguishable, active; antennæ stout, legs long, simple eyes large, rostrum large.

Male	*Female*
2nd Instar—Antennæ and legs stout, body segmentation distinct.	2nd Instar—Legs and antennæ lacking, simple eyes minute, body without apparent segmentation, rostrum functional.
3rd Instar—Legs and antennæ lacking. Much like 2nd instar of female.	3rd Instar—Legs and antennæ lacking, simple eyes minute, body without apparent segmentation, rostrum functional.
4th Instar—Developing legs and antennæ present, rostrum lacking, mesothorax shows traces of future wing pads.	4th Instar—Legs and antennæ lacking, simple eyes minute, body without apparent segmentation, rostrum functional.
5th Instar, Pupa—Developing legs and antennæ long and stout, wing pads broad.	5th Instar, Adult Female—Eyes minute, rostrum lacking, legs and antennæ stout, body segmentation well defined.
6th Instar, Adult—Compound eyes large and projecting, legs stout, antennæ long, fore wings large and functional, rostrum lacking.	

Young are produced oviparously.

(Adapted from Hubbard and Pergande.)

The metamorphosis of the male coccid falls in line with that of the female for the first, and in many respects for the second instar.

Then, as though the somatic memory of Hemipteron inheritance reclaims its own, the insect reverts to the methods of the order to which it belongs and develops antennæ, legs and wings by the external gradual process proper to the Rhychota. In the confusion, however, between the generalized Hemipteron transformation by gradual external development of adult characters, and the specialized tendency of the parasitic coccid toward atrophy of these same characters, the male, attempting both, accomplishes neither in typical shape; but strikes a happy medium all his own by passing through his latter nymphal instars beakless and quiescent, and emerging a queer atom of an insect in possession of remarkable eyes, well developed legs and antennæ, and usually functional wings (albeit there is little left of the hind pair but the costal hooks), but lacking curiously enough the only emblem of Homopteron relationship which his wingless, eyeless,* legless,* antennaless*, mate can boast—the beak*.

The biological urge for overproduction is chiefly provided for, among the coccids, by the great number of eggs deposited rather than by a conspicuous shortening of the life term of the generation. Coccid eggs are typically fertilized though there are many instances of parthenogenetic eggs recorded. Parthenogenesis in the coccids, however, does not seem to function toward a greater number of generations per season as with the aphids but is merely an alternative of certain species. This is also the case with the ovo-viviparous reproduction of those species where the egg undergoes complete development and hatches within the body of the living female; a process which does not carry the significance of the viviparous reproduction of aphids.

Except for those species for which apterous and alate males both occur, polymorphism is not exhibited by the coccids, nor do they have an alternation of generations—one being like another in form and habit. Perhaps nowhere else among the insects, however, do we find a more excessive difference in the two sexes than in the extraordinary dimorphism of the coccids.

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*This, of course, can not be said of the whole family. The female, *Xylococcus betulæ*, for instance, *possesses* eyes, legs and antennæ and *lacks* the beak!

VIII. LIFE CYCLE OF *Aspidiotus perniciosus*.

Fertilized Eggs.

Male and Female

1ST INSTAR (12 days), indistinguishable—Legs, antennæ, rostrum and simple eyes present; active.

Male

2ND INSTAR (6 days)—Eyes large, beak functional, legs and antennæ lacking.

3RD INSTAR (2 days)—Rostrum lacking, developing eyes large, wing pads and developing antennæ and legs all external and free; inactive.

4TH INSTAR (4 to 6 days)—Head, antennæ, legs, wing pads and style are well formed, rostrum lacking.

5TH INSTAR, Adult—2 wings; legs, antennæ and eyes functional, rostrum lacking.

Female

2ND INSTAR (8 days)—Simple eyes, legs and antennæ lacking, rostrum functional.

3RD INSTAR—Adult, produces young for 6 weeks. Legs and antennæ lacking and rostrum functional.

Young are produced ovi-viviparously, the fertilized eggs undergoing development within body of the female. (Sometimes oviparously.)

(Adapted from Pergande, 1895.)

The sedentary habits of the female scales leave the natural dispersal of these insects to the first instar larvæ so that, except for accidental carriers, the spread is characterized by its thoroughness rather than by its breadth.

The most congenial conditions for the coccids are found in warm climates, and there are comparatively but few species whose life cycles are attuned to regions having severe winters.

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5. THE LIFE CYCLE OF THE LEPIDOPTERA.

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Coming at the point in this program between discussions of heterometabolous and holometabolous development, it seems necessary for us to diverge a few moments from the subject as printed, to consider the biological significance of complete metamorphosis.

The structural basis for the distinction between these two types of development has been repeatedly described. Studies histological, morphological, and physiological, have been made on the ontogeny of the different parts of the insect body, in ametabola, heterometabola, and holometabola. Uniformity has been discovered in wing development, cell structure, and body sclerites within each of these groups until we may say that the basis for the three great subclasses of insects rests on a solid foundation in morphology.

The biological significance of these groups, on the other hand, has usually been overlooked. The environmental problems which evolution is called upon to solve, if we may be permitted to express the situation in this way, become immensely complicated as the number of different forms taken on by a single individual increases.

Speaking biologically then, insects without metamorphosis exist in, and are thus adapted to, a single environment, both the form and the surroundings remaining the same throughout the life of the individual. With the arrival of wings, an increase in the number of activities causes an enlargement of horizon and introduces some degree of variety in the character of the